THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[SECOND SERIES.]

No. 80. AUGUST 1854.

VII.—*Researches on the Development of Viviparous Aphides.* By Waldo I. Burnett, M.D., Boston*.

Every naturalist is aware of the remarkable phænomena connected with the viviparous reproduction of Aphides or plant-lice, for their singularity has led them to be recounted in works other than those of natural science, and, from the days of the earlier observers, they have been the theme of a kind of wonder-story in zoology and physiology.

I need not here go over the historical relations of this subject. The queer experiments and the amusing writings of the old entomologists are well known. The brief history of the general conditions of the development of these insects is as follows:—In the early autumn the colonies of plant-lice are composed of both male and female individuals; these pair, the males then die, and the females soon begin to deposit their eggs, after which they die also. Early in the ensuing spring, as soon as the sap begins to flow, these eggs are hatched, and the young lice immediately begin to pump up sap from the tender leaves and shoots, increase rapidly in size, and in a short time come to maturity. In this state it is found that the whole brood, without a single exception, consists solely of females, or rather and more properly, of individuals which are capable of reproducing their kind. This reproduction takes place by a viviparous generation, there being formed in the individuals in question young lice, which, when capable of entering upon individual life, escape from their progenitor and form a new and greatly increased colony. This second generation pursues the same course as the first, the individuals of which it is composed being, like those of the first, sexless, or at least without any trace of the male sex throughout. These same conditions are then repeated, and so on almost indefinitely, experiments having shown that this power of reproduction under such circum-

* From Silliman's American Journal for January 1854.

stances may be exercised, according to Bonnet*, at least through nine generations, while Duvau† obtained thus eleven generations in seven months, his experiments being curtailed at this stage, not by a failure of the reproductive power, but by the approach of winter which killed his specimens; and Kyber‡ even observed that a colony of *Aphis dianthi* which had been brought into a constantly heated room, continued to propagate for four years, in this manner, without the intervention of males, and even in this instance it remains to be proved how much longer these phænomena might have been continued.

The singularity of these results led to much incredulity as to their authenticity, and on this account the experiments were often and carefully repeated; and there can now be no doubt that the virgin *Aphis* reproduces her kind, a phænomenon which may be continued almost indefinitely, ending finally in the appearance of individuals of distinct male and female sex, which lay the foundation of new colonies in the manner just described§.

The question arises, what interpretation is to be put upon these almost anomalous phænomena? Many explanations have been offered by various naturalists and physiologists, but most of them have been as unsatisfactory as they have been forced, and were admissible only by the acceptance in physiology of quite new features.

As the criticism I intend to offer upon some of these opinions will be better understood after the detail of my own researches, I will reserve their future notice until the concluding part of this paper.

My observations were made upon one of the largest species of *Aphis* with which I am acquainted, the *Aphis Caryæ* of Harris‖. While in Georgia, this last spring, it was my good fortune that myriads of these destroyers appeared on a hickory which grew near the house in which I lived. The number of broods on this tree did not exceed three, for with the third series their numbers were so great that their source of subsistence failed and they gradually disappeared from starvation. The individuals of each

* Traité d'Insectologie, ou Observations sur les Pucerons, 1745.

† Mém. du Mus. d'Hist. Nat. xiii. p. 126.

‡ Germar's Magaz. d. Entomol., 1812.

§ For details of experiments by which Bonnet's original results were verified, see Réaumur, Mémoires, iii. Mém. 9 and 11, and vi. Mém. 13. Also, DeGeer, Mémoires, iii. ch. 2, 3. Curtis, Trans. Linn. Soc. vi.; Philos. Trans. 1771. Sauvages, Journ. de Physique, i. Dutrochet, Mémoires, ii. p. 442. See also the more modern writers, and especially Kirby and Spence, Introduction to Entomology, iv. p. 161.

‖ A Treatise on some of the Insects of New England which are injurious to Vegetation, 2nd ed. 1852, p. 208. As Dr. Harris says, it is probably *Lachnus* of Illiger (*Cinara* of Curtis).

brood were, throughout, of the producing kind, no males having been found upon the closest search; they were all, moreover, winged; and those few that were seen without these appendages appear to have lost them by accident. I mention this fact especially, since it has been supposed by naturalists that the females were always wingless, and therefore that the winged individuals, or the males, appeared only in the autumn*.

The first brood, upon their appearance from their winter hiding-places, were of mature size, and I found in them the developing germs of the second brood quite far advanced. On this account it was the embryology of the third series or brood alone that I was able to trace in these observations.

A few days after the appearance of these insects, the individuals of second brood (B), still within their parents (A), had reached two-thirds of their mature size. At this time the arches of the segments of the embryo had begun to close on the back, and the various external appendages of the insect to appear prominently; the alimentary canal had been more or less completely formed, although distinct abdominal organs of any kind belonging to the digestive system were not very prominent. At this period, and while the individuals of generation B are not only in the abdomen of their parent A, but are also enclosed, each, in its primitive egg-like capsule,—at this time, I repeat, appear the first traces of the germs of the third brood (C).

These first traces consist of small egg-like bodies arranged two, three, or four in a row, and attached in the abdomen at the locality where the ovaries are situated in the oviparous forms of these animals.

These egg-like bodies consisted either of single nucleated cells, of $\frac{1}{3000}$th of an inch in diameter, or a small number of such cells enclosed in a simple sac. These are the germs of the third generation; they increase with the development of the embryo in which they have been formed, and this increase of size takes place, not by a segmentation of the primitive cells, but by the endogenous formation of new cells. After this increase has gone on for a certain time, these egg-like bodies appear like little oval bags of cells—all these component cells being of the same size and shape, there being no cell which is larger and more prominent than the rest, and which could be comparable to a germinative vesicle. While these germs are thus constituted, the formation of new ones is continually taking place. This occurs by a kind

* See Westwood, An Introduction to the modern Classification of Insects, &c. London, 1839, ii. p. 438; but especially Owen, Parthenogenesis, &c., p. 23, note, and p. 59, note, where he says, "Many of the virgin viviparous Aphides acquire wings, but never perfect the generative organs!"

of constriction-process of the first germs, one of their ends being pinched off, as it were, and in this way what was a single sac, is changed into two which are attached in a moniliform manner. The new germ thus formed may consist of even a single cell only, as I have often seen, but it (the germ) soon attains a more uniform size by the endogenous formation of new cells within the sac by which it is enclosed. In this way the germs are multiplied to a considerable number, the nutritive material for their growth being apparently a fatty liquid with which they are bathed, contained in the abdomen, and which is thence derived from the abdomen of the first parent.

When these germs have reached the size of $\frac{1}{300}$th of an inch in diameter, there appears on each, near one end, a yellowish vitellus-looking mass or spot, which is composed of large yellowish cells, which in size and general aspect are different from those constituting the germ proper. This yellow mass increases *pari passu* with the germ, and at last lies like a cloud over and concealing one of its poles. I would also insist on the point that it does not extend itself gradually over the whole germ-mass, and is therefore quite unlike a true germinative vesicle or a proligerous disc. When the egg-like germs have attained the size of $\frac{1}{150}$th of an inch, there distinctly appears the sketching or marking out of the future animal. This sketching consists at first of delicately-marked retreatings of the cells here and there, but which soon become more prominent from furrows, and at last the whole form of the embryo stands boldly out. As the whole idea and form of the insect is thus moulded out of a mass of cells, it is evident that the separate parts which then appear, such as the arches of the segments, the extremities and the oval apparatus, consist at first only of rows of simple cells. This point is here beautifully prominent, and nowhere have I observed finer illustrations of the cell-constitution of developing forms.

The development thus proceeding, each part of the dermoskeleton becomes more and more distinct, and the increase of size of the whole is attained by the constant development of new cells. During this time, the yellow vitellus-looking mass, situated at one of the poles of the embryo, has not changed its place; it has increased somewhat in size, but otherwise appears the same. When the development has proceeded somewhat further, and the embryo is pretty well formed, the arches of the segments, which have hitherto remained gapingly open, appear to close together on the back, thereby enclosing this vitellus-looking mass within the abdominal cavity.

It is this same vitelloid mass thus enclosed that furnishes the nutritive material for the development of new germs which would be those of the fourth brood, or D; this development of germs here commences with the closing up of the abdominal cavity, and the same processes which we have just described are again repeated.

The details of the development subsequent to this point are like those of the development of ordinary insects or of the Articulata in general; and although this ovoid germ has at no time the structural peculiarities of a true ovum—such as a real vitellus, a germinative vesicle and germinative dot; yet, if we allow a little latitude in our comparison, and regard the vitellus-looking mass as the *mucous*, and the germ-mass proper as the *serous* fold of the germinating tissue, as in true eggs—if, I repeat, we can admit this comparison of parts, then the analogy of development between these germs and true eggs of insects may be traced in considerable detail.

This comparison I have been inclined to admit at least in part, from the striking resemblance of these developing forms at certain stages, with the embryological forms of spiders as they have been figured by Herold* and as I have myself traced them. When, in spiders, the serous fold of the germinating tissue has extended so as to cover two-thirds of the developing form, leaving the vitelline mass on the dorsal surface near one of the poles, the whole embryo quite resembles that of a developing Aphis just before the arches of the segments close up on the back.

With this view of the relative parts of the germ, the following would be the details of the development of the different systems, and in the noticing of which I shall follow Kölliker†.

1. The germinating tissue consists of two parts; a serous and mucous fold.

2. The abdominal plates arise from the serous fold, sprout out towards the vitelloid mass, pass over it and unite on the dorsal surface of the future animal; on the opposite side are formed plates which do not unite, but are formed into the hind legs.

3. The wings are the lateral limbs.

4. The first traces of the abdominal column appear in the chain of abdominal muscles situated between the nerves and the intestinal canal.

5. The nervous system in all its parts arises from the serous fold, as well also as the organs of sense.

6. The mucous fold, or the vitellus-looking mass, serves no purpose in the formation until the closing in of the visceral plates.

7. Thus enclosed in the abdominal cavity, it is not transformed

* De Generatione Aranearum in ovo. Marbourg, 1824.

† Observationes de prima Insectorum genesi adjecta Articulatorum evolutionis cum Vertebratorum comparatione. Diss. Inaug. Scr. Alb. Kölliker. Turin, 1842. A work replete with facts and interesting suggestions.

directly into the intestinal canal, but simply furnishes the material from which the component cells of the said canal and its hepatic diverticula are formed. It also furnishes the material from which the new germs are formed, as already shown.

8. The heart is formed on the dorsal aspect between the mucous and serous folds. In this way the details of development closely correspond with those of the embryology of the other Articulata which I have studied; and the subject is all the more interesting, as the germ-masses, from which such development occurs, in no way and at no time structurally resemble true eggs.

When the embryo is ready to burst from its developing capsule and make its escape from the abdomen of its parent, it is about $\frac{1}{16}$th of an inch in length, or more than eight times the size of the germ at the time when the first traces of development were seen. From this it is evident that, even admitting that these germ-masses are true eggs, the conditions of development are quite different from those of the truly viviparous animals; such as for instance in *Musca, Anthomyia, Sarcophaga, Tachina, Dexia, Miltogramma,* and others among Dipterous insects*; or in the viviparous reptiles,—for in all these cases of ordinary viviparity, the egg is simply hatched in the body instead of out of it. The egg, moreover, is formed exactly in the same way as though it was to be deposited, and its vitellus contains all the nutritive material required for the development of the egg until the coming forth of the new individual. The abdomen of the mother serves only as a proper nidus or incubatory pouch for its full development. This is true of all the ovo-viviparous animals whatsoever†. With the viviparous Aphides, on the contrary, the developing germ derives its nutritive material from the fatty liquid in which it is bathed, and which fills the abdomen of the parent‡. The conditions of development here therefore are more like those in Mammalia, and the whole animal may, in one sense, be regarded as an individualized uterus filled with germs, for the digestive canal, with its appendages, seems to serve only as a kind of laboratory for the conversion of the succulent fluids which the animal extracts from the tree on which it lives, into this fatty

* See Siebold in Froriep's Neue Notiz. iii. p. 337, and in Wiegmann's Arch. 1838, i. p. 197; also his Observat. quæd. Entom. &c., p. 18.

† It is true that in the Scorpionidæ the eggs are developed in the ovary, but there is no reason to suppose that the conditions are here different from those of the viviparous Diptera. In *Oribates*, also, the eggs are developed in a kind of uterus situated directly above the ovipositor, but this appears to be only an incubatory pouch.

‡ This fatty matter forms beautiful crystals of margarine, and the crystallization may easily be seen to take place. The forms exactly resemble those given by Robin and Verdeil, Traité de Chim. Anat. et Physiol. pl. 38. fig. 2 *h*. Paris, 1853.

liquid from which the increase and development of the germs take place.

When the young animal has reached its full development as an embryo, it bursts from its encasement and appears to escape from the abdomen of its parent through a small opening (*porus genitalis*) situated just above the anus. In the species under consideration it generally remains clinging on the back of the parent until its external parts are dry and it is able to begin life for itself. Each parent here produces from eight to twelve individuals, and if this rapid increase is continued undisturbed, through seven to nine broods, we cannot wonder at the countless numbers which appear from so few original individuals*.

Such are the details of the embryological development of the so-called viviparous Aphides, as far as I have enjoyed opportunities for their study. We will now refer for a moment to the special points which have here been made out. In the first place, it is evident that *the germs which develope these forms are not true eggs*. They have none of the structural characteristics of eggs, such as a vitellus, a germinative vesicle and dot; on the other hand, they are, at first, simple collections, in oval masses, of nucleated cells. Then again, they receive no special fecundating power from the male, as is the necessary preliminary condition of all true eggs; and, furthermore, the appearance of the new individual is not preceded by the phænomena of segmentation, as also is the case with all true eggs. Therefore their primitive formation, their development, and the preparatory changes they undergo for the evolution of the new individual, are all different from those of real ova†.

Another point is, *these viviparous individuals have no proper ovaries and oviducts*. Distinct organs of this kind I have never been able to make out. The germs are situated in moniliform rows, like the successive joints of confervoid plants, and are not enclosed in a special tube. These rows of germs commence, each, by a single germ-mass which sprouts from the inner surface of the animal, and which increases in length and in the number

* Réaumur has shown that in these animals the rate of increase is so great, that in five generations or broods only one Aphis may be the progenitor of five billion nine hundred and four million nine hundred thousand (5,904,900,000) descendants; we may well ask, what would be the number of descendants where the broods were extended to eleven!!—See Kirby and Spence, Introduction to Entomology, i. p. 175.

† Milne-Edwards thinks he has found true *ova* and ovaries in the viviparous forms of these animals. (Quoted by Dr. Carpenter in Brit. and For. Med. Chir. Rev. 1849, iv. p. 443.) I think he must have been deceived, as I was at first, by the general appearances, which, unless carefully examined, closely resemble those of true oviparous individuals.

of its component parts from the successive formation of new germs by a constriction-process as already mentioned. Moreover, these rows of germs, which, at one period, closely resemble in general form the ovaries of some true insects, are not continuous with any uterine or other female organ, and therefore do not at all communicate directly with the external world. On the other hand, they are simply attached to the inner surface of the animal, and their component germs are detached into the abdominal cavity as fast as they are developed, and then escape outwards through a *porus genitalis,* exactly as is the case with the eggs of fishes*. Here, then, comes the important question, What interpretation shall we put upon these reproductive parts—these moniliform rows of germs? Ignoring all existing special theories relating to reproduction, the observing physiologist would be left no alternative but to regard them as *buds,* true gemmæ, which sprout from the inner surface of the Aphis, exactly like the buds from the external skin of a Polype†.

Before proceeding to a discussion of the relations of this important conclusion to which we have just arrived, it may be well to refer to the views of others upon the exact signification of these singular reproductive phænomena.

Those old entomologists, such as Bonnet, Réaumur, DeGeer, &c., who were the first to observe, besides verifying beyond all doubt, these peculiar phænomena, all believed that each brood constitutes a separate generation, and that the reproduction takes place by true ova, as in the common generative act of other insects. This wide deviation from the ordinary course of nature, as it seemed to them, they attempted to explain and reconcile by various theories. Thus Réaumur‡ affirmed that these viviparous individuals were androgynous; and, in later times, Léon Dufour§, who knew too well the anatomical structures of insects to believe with Réaumur that they could be hermaphrodites, referred these phænomena to spontaneous or equivocal generation.

Morrem||, who made somewhat extended researches on the

* These observations of mine on the special anatomy of the reproductive parts of viviparous Aphides agree with those of Siebold, who studied the subject with much care several years since. See Froriep's Neue Not. xii. p. 308. Siebold, however, regarded them as true ovaries and oviducts, but without any of the usual appendages which are found in the true oviparous Aphides.

† I would insist upon this wide and important distinction between buds and ova. The structure and conditions of all ova are the same, and there is no passage between them and buds. But this point will be enlarged upon hereafter.

‡ *Loc. cit.* Mémoires.

§ Recherches Anat. et Physiol. sur les Hémiptères. Paris, 1833.

|| Anat. de l'*Aphis persicæ,* in the Ann. d. Sc. Nat. v. 1836, p. 90.

anatomy of *Aphis persicæ*, and especially of its generative organs, advanced the novel theory, that these broods were developed in the body of the virgin parent, by a previously organized tissue becoming individualized and assuming an independent life, exactly, as he believed, to be the case with Entozoa. To each and all of these views, it scarcely need be said that they would be wholly inadmissible according to the present established doctrines of physiological science, even had we no directly controverting observations.

But there are other explanations or views which deserve more attention. The first of these is that advanced by Kirby and Spence*. According to them, "One conjunction of the sexes suffices for the impregnation of all the females that in a succession of generations spring from that union." In support of the reasonableness of this hypothesis, they quote several instances which they regard as of analogous character; thus, they say in regard to the hive-bee, that "a single intercourse with the male fertilizes all the eggs that are laid for the space of two years."

In this connection should be mentioned the similar hypothesis advanced for a like purpose by Jourdan†. According to him many Lepidoptera lay fertile eggs when completely isolated from the males: such are, *Euprepsia casta, Episema cæruleocephala, Gastropacha potatoria, G. quercifolia* and *G. pini, Sphinx ligustri, Smerinthus populi*, and *Bombyx querci*.

But all these cases have really no strict analogy with that of the Aphides in question; for there is not, as with these last, a succession of innately fertile individuals, but only females which are capable of producing several broods from a single coitus, or after having been long removed from the males, which may even then be dead‡. Late researches upon the minute anatomy of the generative organs of insects have furnished results by which these phænomena, seemingly strange at first, can be explained. All these insects which are thus capable of laying fecundated eggs

* Introduction to Entomology, iv. p. 161.

† Manuel de Physiologie, par J. Müller, Trad. de l'Allemand, etc. par A. J. L. Jourdan. Deux. éd. rev. et annot., par E. Littré, ii. p. 599, note.

‡ Siebold has made observations upon allied phænomena occurring in the Psychidæ, which are of no little interest. He has shown that in the genera *Psyche* and *Fumea*, the alleged reproduction, *sine Lucina*, is unfounded—these insects having well-formed internal genital organs, and the male being adapted to impregnate the female while the latter is in her case. But in the genus *Talæporia*, Siebold has shown that there is propagation *sine concubitu*, exactly as occurs with the Aphides. See Ueber die Fortpflanzung der Psyche: Ein Beitrag zur Naturgeschichte der Schmetterlinge, in Siebold and Kölliker's Zeitsch. i. 1849, p. 93: but, for his last researches on *Talæporia*, see his Bericht üb. d. entomol. Arbeiten d. schles. Gesellsch. im J. 1850; or its English transl. in the Trans. of the Ent. Soc. N. S. i. p. 234.

again and again after the first impregnation, have a *receptaculum seminis* connecting with the oviduct, in which the semen is deposited during coition, and where it may be preserved without losing its vitalizing power for several months*. Thus, by this provision, the males, having copulated with the females in the autumn, may immediately die, while these last, hibernating, produce in the spring fertile ova; and in the instance of the *Bombus americana*, such a coition suffices for all the three broods which are produced the ensuing summer.

Another explanation of these curious phænomena, and which has attracted some attention, as well from its singularity as from the eminence of its propounder, is that of Owen, advanced in his Hunterian Lectures in 1843†.

He affirms that the larval Aphides are productive in virtue of the successive continuation from brood to brood of a portion of the primitively fertilized germ, and which material product or leaven is not exhausted until nine to eleven generations. I will quote his own language: "In the Aphides the corresponding vitelline cells retain their share of the fecundating principle (which was diffused through the parent egg by the alternating, fissiparous, liquefactive, and assimilative processes) in so potent a degree, that a certain growth and nutritive vigour in the insect suffice to set on foot in the ovarian, nucleated cells, a repetition of the fissiparous and assimilative process, by which they transform themselves in their turn into productive insects; and the fecundating force is not exhausted by such successive subdivision until a 7th, 9th, or 11th generation." This same doctrine, the successive inheritance of a portion of the primary germ-mass from brood to brood, and by means of which the fertile germs are continued, —this doctrine, I say, is repeated in full in this author's work on Parthenogenesis, and I will here quote one sentence, not only in illustration of this, but to show how different his own observations on the development of these animals are from mine, just described. He says, "One sees such portion of the germ-mass

* For many details on this subject of the *receptaculum seminis*, see Siebold, Müller's Arch. 1837, p. 392; also in Wiegmann's Arch. 1839, i. p. 107 (*Vespa*), and in Germar's Zeitsch. ii. (1840) p. 442 (*Culex*). See also Stein, Vergleich. Anat. &c. 1847, p. 96, 112. I cannot but believe that the anomalous reproductive conditions of the Cynipidæ will, at last, have a solution equally satisfactory. See Hartig, Germar's Zeitsch. ii. p. 178, and iv. p. 395. See also Siebold and Stannius's Comparative Anatomy, transl. i. sect. 348, notes 1 & 4.

† Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals, &c. London, 1843, p. 233. This explanation is lately insisted upon (strange to relate) in his recent work "On Parthenogenesis, or the successive production of procreating individuals from a single ovum." London, 1849.

taken into the semitransparent body of the embryo Aphis, like the remnant of the yolk in the chick. I at first thought it was about to be enclosed in the alimentary canal, but it was not so. As the embryo grows, it assumes the position of the ovarium, and becomes divided into oval masses and enclosed by the filamentary extremities of the eight oviducts. Individual development is checked and arrested at the apterous larval condition. It is plain, therefore, that the essential condition of the development of another embryo in this larva is the retention of part of the progeny of the primary impregnated germ-cell." (p. 70.)

This view of Owen, so ingeniously advanced, and which he has made subservient for the chief support of his new doctrine of Parthenogenesis, is indeed plausible and seems at first satisfactory; but, as I hope to show, it will not bear analysis.

In the first place, it is evident that Owen does not recognise any physiological difference between a *bud* and an *ovum*; this is clear from what he remarks in the first quotation, but in his work on Parthenogenesis he has said so in as many words. "The growth by cell-multiplication producing a bud, instead of being altogether distinct from the growth by cell-multiplication in an egg, is essentially the same kind of growth or developmental process." (p. 45.)

Here is a fundamental error, which, if not removed, will obscure all our views of the physiology of reproduction. I have already insisted upon the necessity of this broad distinction between these two forms,—a necessity based not only upon differences of anatomical constitution, but also upon physiological signification. An *Ovum* is the exclusive product of an individual of the female sex, and is always formed in a special organ called the ovary. It is the particular potential representative of the female, and has its ulterior development only from its conjunction with a corresponding element of the opposite or male sex; and zoology presents no instance where there is development from eggs, unless these conditions of the two sexes are fully carried out.

A *Bud*, on the other hand, is simply an offshoot from the form on which it rests, a portion of the animal capable of individual development. It sustains, therefore, no relations to sex, and, in truth, is widely separated in its ulterior signification from that cycle of processes conceived in a true oviparous reproduction.

All physiologists who have carefully studied embryological and developmental processes must feel the correctness and importance of this distinction, which lies in realities and not in words.

It is true, that a bud and an ovum are composed each of the same elements,—simple nucleated cells; but in one, these cells are simply in a mass, while in the other, they have, throughout the animal kingdom, high or low, a definite and invariable arrangement. Then again as to the constitution of each and both being, on the whole, of nucleated cells, it may be said, that it could hardly be conceived to be otherwise, for nucleated cells are the elementary components of all functional organized forms; and it may be added, moreover, that he knows little of the highest physiology who has not learned that widely different teleological significations may be concealed beneath isomorphic animal forms.

I have thus dwelt rather lengthily upon this point because I think it is a vital one in our subject, and the possession of clear ideas thereon will be found singularly conducive to our correct appreciation of the whole class of anomalous phænomena under discussion. But we will revert to the subject of Owen's hypothesis.

As to the chief point in this hypothesis, the continuation of the primary germ-mass as a leaven, from brood to brood, it requires but little thought to perceive that it is physically impossible. I would first allude to Owen's statement, quoted above, that a portion of the germ-mass is taken into the abdomen of the embryo Aphis, and, as he thinks, assumes, without any change, the position of the ovarium. By this he refers, undoubtedly, to the vitellus-looking mass I have described in my observations, and according to which, also, it appeared to serve only as the nutritive material out of which the digestive organs and the germs are formed. Moreover, I feel quite sure that the germ-cells are new cells formed in the abdomen, and not those derived from the parent.

But the point I wish to enforce is, that even admitting that individuals B may contain an *actual residue* of individuals A, it is clearly evident that this succession must stop with brood B; for these residual germ-cells which compose B in its earliest condition are lost in the developmental processes, and the germs of individuals C, which are found in B, are each, primarily, nucleated cells formed *de novo*, as I have observed and above described. With these observed conditions of development, it is impossible for the individuals of the successive broods to inherit the original spermatic force in the continuation of the original cells.

The hypothesis of Owen, therefore, plausible and ingenious as it may seem, does not appear to me to accord either with observed facts, or with the soundest physiology of the reproductive processes. I may here remark also, that his doctrine of Parthenogenesis, based as it is upon the conditions of the hypothesis in question, cannot, as such, be sustained, for the same reasons, and all its phænomena would appear to find their solution either in Steenstrup's doctrine of "Alternation of Generations," so-called, or in the conditions of true gemmiparity,—admitting, provisionally, that Steenstrup's doctrine and gemmiparity include really different physiological conditions.

But the most important explanation advanced, and the last which I shall notice, is that offered by Steenstrup* in his doctrine of the "Alternation of Generations," and of which it forms a chief support. The details of this peculiar doctrine of Steenstrup I need not here furnish; they are well known to all physiological anatomists. Its features, however, may be expressed in a formula-like manner. Individuals A produce true fecundated eggs, from which are hatched individuals B, which are unlike their parents in all zoological respects, but in which are developed spontaneously and without any reference to sex, germs which ultimately become individuals like A, and so the cycle of development is completed. These intermediate individuals, B, Steenstrup has termed nurses (*Amnen*), and he regards them as distinct animals subservient for a special end; he therefore considers that B constitutes a real generation.

Instances of such phænomena are found in the lower orders of the animal kingdom—Polyps, Acalephs and Worms; and late research has shown that they are more or less common throughout the whole of the Invertebrata.

The difference between alternation of generation and metamorphosis is too marked to require illustration; in the latter there is the same individual throughout, and the developmental processes, although concealed beneath different exteriors, are regular and normal; with the former, however, this chain of development is broken by one form being developed in another, this intermediate form serving as a stepping-stone for a higher and ulterior development. Another important point in this alternate reproduction, is, that in each new change some real progress is made—the nursing-form being manifestly inferior to the individual to which it gives rise.

Steenstrup regards the Aphides as furnishing the most perfect examples known of nursing individuals, and, on the whole, as constituting typical illustrations of the doctrine he has advanced†.

But if this doctrine implies conditions other than those which belong to true gemmiparity, it does not appear to me that it has any support in the phænomena in question of the Aphides. And although I am inclined to believe, as I shall soon show, that all these phænomena, essentially, may be of the same nature, yet there can be no doubt that the manifestations are here somewhat pecu-

* On the Alternation of Generations, or the Propagation and Development of Animals through Alternate Generations; a peculiar form of fostering the young in the lower classes of Animals. Transl. by the Ray Society. London, 1845, *passim*.

† See Steenstrup, *loc. cit.* p. 112.

liar. With the Aphides there is no real morphological progress made in each brood, for the viviparous individuals are, zoologically, as perfect in every way as those which are oviparous, except in their want of true sexual generative organs. I have shown that, in the one species here described, they had well-developed wings like the true sexual individuals. Moreover, each brood, from the first to the last inclusive, is merely a repetition of the same. But these conditions are external and œconomical, and, instead of offering these prominent examples as evidence against the validity of Steenstrup's doctrine, I would rather present them as broadly indicating that, after all, this doctrine in question involves no conditions excepting those belonging to a modified form of gemmiparity. All the instances of Polyps, Acalephs, Worms, Insects, &c., would then be classed in the same category, and the variations in manifestation would belong rather to the œconomical relations of the animal, than to any intrinsic difference of physiological process. Thus the Distoma-nurses, instead of being developed to a condition resembling at all their parent, remain persistent on a low form, and not only is their whole zoological character undeveloped, but they also experience morphological changes from the developmental process which immediately go on within them. All this is in perfect keeping with their œconomy as animals, for the low order of their conditions of life does not necessitate a higher and more truly zoological form of these nurses from which are to be developed the true animals; were it otherwise, I cannot but believe that both the nurses and the grand-nurse of Distoma would quite resemble the original animals. In the case of the Aphides, the œconomical conditions are different, and finely illustrate this point.

The Aphis-nurse, in virtue of its very typical structure as an insect, must live under higher conditions, and so its development, zoologically, proceeds to a corresponding point; this point is where it, as an insect and as an Aphis, can furnish the nutritive material for the development of its endogenous germs.

Herein, then, would appear to consist the prominent morphological differences observed in this category of phænomena, and I need not labour further to show that they are irrelevant of the primary essential conditions of these curious processes.

Such appears to me to be the highest, both physiological and zoological, interpretation that can be advanced for these phænomena which Steenstrup has so ingeniously collected and collated; and to advance the view that these intermediate individuals or nurses are not intrinsically and zoologically the same as their parents, but furnish examples of how dissimilar animals may arise from a common stock—to put forth this view, I say, is to advocate a doctrine in physiology as mischievous as it is deeply erroneous. I think, therefore, that the doctrine of Steenstrup may prove to be unfounded as far as it would involve, intrinsically, new phænomena in the processes of reproduction; and, as I have said on a preceding page, all its conditions may find their illustration and solution in the various phases of gemmiparity*.

If in this discussion of some of the highest relations of physiology, we have not wandered too far from our subject proper which we have thereby sought to illustrate indirectly, we will revert to the thread of its discourse for a few concluding remarks.

The final question now is, what is the legitimate interpretation to be put upon the reproductive phænomena of the Aphides we have described? My answer to this has been anticipated in the foregoing remarks. I regard the whole as constituting only a rather anomalous form of gemmiparity. As already shown, the viviparous Aphides are sexless; they are not females, for they have no proper female organs, no ovaries and oviducts. These viviparous individuals therefore are simply gemmiparous, and the budding is here internal instead of external as in the Polyps and Acalephs; it moreover takes on some of the morphological peculiarities of oviparity; but all these dissimilar conditions are œconomical and extrinsic, and do not touch the intrinsic nature of the processes concerned therein.

Viewed in this way, the different broods of Aphides cannot be said to constitute as many true generations, any more than the different branches of a tree can be said to constitute as many trees; on the other hand, the whole suite from the first to the last constitute but a single true generation. I would insist upon this point as illustrative of the distinction to be drawn between *sexual* and *gemmiparous* reproduction. Morphologically, they have, it is true, many points of close resemblance; but there is a grand physiological difference, the true perception of which is deeply connected with our highest appreciation of individual animal life†. A true generation must be regarded as resulting only from the conjugation of two opposite sexes—from a sexual pro-

* This statement is made perhaps more strongly and exclusively than the present state of our knowledge would warrant, but I throw it out much in a suggestive way. There is no subject in physiology more interesting and comprehensive than that of *Gemmation*; the important question now is,—does it, as an individual process, embrace all the categories of phænomena treated by Lovén, Steenstrup, &c., these phænomena varying extrinsically, according to œconomical conditions, or do they (the phænomena) imply something beyond and dissimilar from gemmation?

† In this view, as well as in several others herein discussed, I am pleased to say that I have the support of so learned a physiologist as Dr. Carpenter. See his Review "On the Development and Metamorphoses of Zoophytes," in the Brit. and Foreign Med. Chir. Rev. 1848, i. p. 183; and "On Reproduction and Repair," in ibid. 1849, ii. p. 419.

cess in which the potential representations of two individuals are united for the elimination of one germ. This germ-power may be extended by gemmation or by fission, but it can be formed only by the act of generation, and its play of extension and prolongation by *budding*, or by division, must always be within a certain cycle, and this cycle is recommenced by the new act of the conjugation again of the sexes.

In this way, the dignity of the ovum as the primordium of all true individuality is maintained; and the axiom of Harvey, *omne vivum ex ovo*, stands as golden in physiology. The buds may put on the dress and the forms of the ovum, but these resemblances are extrinsic, and in fact only an inheritance from their great predecessor.

These phænomena, thus interpreted, furnish an excellent key to many others which have long been regarded as anomalous, in the history of development.

I refer here to the so-called hibernating eggs (*Wintereier*) which are found in many Invertebrates. These I have not seen, but they have been carefully described by several very trustworthy observers. These so-called eggs consist of oval masses or cells invested with a capsule, but in which no germinative vesicle and dot have ever been seen. Structurally, therefore, they do not resemble eggs, and it is from their form and ulterior development only that they have received this name. Moreover, they sustain none of the usual relations of eggs to the sexual organs, and, as far as I am aware, no one has witnessed their development in the ovaries. These bodies have been observed in *Hydatina** and *Notommata*† among the Infusoria; in *Lacinularia*‡ among the Rotatoria; and in *Daphnia*§ among the Crustacea. In all these instances they hatch without the aid of the male, the existence of which sex was once doubted from its unfrequent appearance.

Now I regard these hibernating eggs as merely egg-like *buds* exactly corresponding to the germs of the viviparous Aphides. In other words, there are in the animals I have just mentioned, certain individuals which reproduce by buds which are developed under rather anomalous conditions; and I will add in conclusion,

* Ehrenberg, Die Infusionsthierchen, p. 413.

† Dalrymple, Philos. Trans. 1849, p. 340.

‡ Huxley, Quarterly Journ. Micr. Sc. 1852, i. p. 13.

§ Müller, Entomostraca, p. 84. tab. 11. fig. 9–11, tab. 12. fig. 5. Also, Ramdohr, Beiträge zur Naturgesch. einiger deutschen Monokulus-Arten, 1805, p. 28; Strauss, Mém. sur les Daphnia, in the Mém. du Mus. d'Hist. Nat. v. p. 413. pl. 29; Jurine, Histoire des Monocles, 1820, p. 120. pl. 11. fig. 1–4. Jurine calls these aggregated eggs "La maladie de la selle." There is, moreover, reason to believe that these anomalous reproductive conditions occur in nearly all the Entomostraca: see Siebold and Stannius's Comparative Anat., my transl. vol. i., my note under sect. 292, note 4.

that I suspect that this gemmiparous mode of reproduction will be found to be far from uncommon among most of the Invertebrata, when our researches into the history of their development shall have been more widely extended*.

P.S.—I regret that I should not have seen until now, when this paper is concluded, the important writings of Leydig on the subject under discussion. In his article "Einige Bemerkungen über die Entwickelung der Blattläuse," in Siebold and Kölliker's Zeitschr. f. wiss. Zool. 1850, ii. p. 62, he speaks of his former observations in the Isis, 1848, iii. p. 184. These I have not seen, neither also a work to which he refers, of J. Victor Carus (Zu näheren Kenntniss des Generationswechsels, Leipzig, 1849). Leydig, in his criticism of Carus's views, expresses the opinion that the development of the viviparous Aphides is, histologically, like that of the Articulata in general. According to him, also, the germ-bodies undergo processes corresponding to those of impregnated eggs. These statements of Leydig, who is an excellent observer, have induced me recently to repeat my observations; but this afforded the same results as before, viz. that the germ-bodies out of which are developed the viviparous Aphides have no true histological identity with eggs.

P.S.† Since the publication of this paper, I have enjoyed the opportunity of making this series of investigations more complete, by an examination of the terminal or last brood which appears at the end of autumn.

This terminal brood has hitherto been considered, as far as I am aware, to be composed exclusively of males and females, or, in other words, of perfect insects of both sexes. I was surprised, therefore, on examining the internal organs of the non-winged individuals, to find that many of these last were not females

* Notice may here be given of some curious observations, which Filippi (Ann. Nat. Hist. ix. June 1852, p. 461) has furnished on the development of the Pteromalidæ. A *Pteromalus* lives in the ova of *Rhynchites betuleti*; in each of these ova there is seen, soon after its deposit, a minute infusorial animal, with a tail by which it moves briskly about among the vitelline cells. It soon ceases to move, however, and in its interior appears a vesicle which increases and changes into a larva which is that of *Pteromalus*; this larva becomes a pupa, and, after eight or ten days, changes to the perfect insect which escapes from the ovum. If these observations are verified, we have here a case exactly like that of the Aphides, excepting that, like the *Distoma*, the intermediate budding form is very low, and takes on none of the zoological peculiarities of the parent. But these statements need corroboration, for they do not agree with the history of other species of *Pteromalus* whose development is well known. See also the wonderful gemmiparous phænomena related by Siebold of *Gyrodactylus*; Siebold and Kölliker's Zeitschr. f. wiss. Zool. i. 1849, p. 347.

† Silliman's Journal for March.

proper, but simply the ordinary gemmiparous form already described. Moreover, so great was the similarity of appearance between these two forms—true females and gemmiparous individuals—that they could be distinguished only by an examination of their internal genitalia. Among the proper females there were, besides those which were filled with eggs or had already deposited them, other individuals in which the ovaries were but feebly developed, or at least, in which no mature eggs had been formed. An opportunity was thereby afforded me to examine the structural differences between the true ovaries and their *quasi* representatives—the bud-like processes. The true ovaries had their usual, well-known structure—multilocular tubes containing nucleated cells which are probably the undeveloped germs; the bud-like processes, on the other hand, consisted of a row of cell-masses, oval and connected by a kind of peduncle, as described in detail in the preceding paper. These wide differences have, more than ever, persuaded me of the morphological dissimilarity of these two kinds of reproducing parts in this animal. It seems to me then that the real intrinsic difference between an ovum and a bud lies as deep as the conditions of sex itself, notwithstanding the latter often has, as in the present case, for instance, some of the morphological characteristics of the former.

The appearance of sexless, gemmiparous individuals in the terminal brood would seem to indicate, moreover, that the conditions which determine the appearance of individuals usually exclusively male and female, are not, perhaps, referable to the fact of this being the last brood, but rather to relations of warmth and nutrition. This view is rendered more probable by the fact of the variation in the number of broods between the first and last, observed in the same species in different years—ranging between seven, nine, eleven or more. Moreover, Kyber, as quoted already in the preceding paper, by nursing continually in a warm room a collection of *Aphis dianthi*, keeping about them a summer temperature, succeeded in continuing uninterruptedly the series of sexless or gemmiparous individuals for four years. There are many other facts in insect life that indicate in like manner some direct relation between temperature and nutriment, and definite sexual development. The subject is as important as it is interesting in physiology, and these very animals will, perhaps, subserve the successful studyof the primary morphological conditions of sex.